LXII.—*On the Systematic Position and Classification of the Gadoid or Anacanthine Fishes.* By C. Tate Regan, B.A.

In the order Anacanthini Dr. Günther * included those fishes which were brought together by the definition "Vertical and ventral fins without spinous rays; ventral fins, if present, jugular or thoracic; air-bladder, if present, without pneumatic duct." Of these the Ammodytidæ are now usually regarded as allied to the Scombresocidæ, whilst the remaining families have been included within the Acanthopterygii by most modern authors. In Messrs. Jordan and Evermann's 'Fishes of North America' † we find that the Lycodidæ, Brotulidæ, Ophidiidæ, &c. are considered to be degraded forms allied to the Blennies, whilst the Gadidæ and Macruridæ are placed next to them, being, however, distinguished by the foramen between scapula and coracoid, and the Pleuronectidæ form a third group, whose nearest relations are stated to be probably with the Gadidæ.

In recent papers Mr. Boulenger ‡ has shown that the Pleuronectidæ are nearer to the Cyttidæ than to any other living fishes, and also that the Trachinidæ, Callionymidæ, and Nototheniidæ resemble the Gadidæ and Macruridæ in the position of the scapular foramen, on which account, and taking into consideration the jugular position of the ventrals, he would associate all the Gadoid, Trachinoid, Blennioid, and Batrachoid fishes in one division of the Acanthopterygii,—Jugulares.

The importance of the position of the scapular foramen had, however, been overestimated, for the same author § has since discovered that *Trematomus* differs from all the other Nototheniidæ in having the foramen entirely within the scapula. I find a similar instance in the Macruridæ, a species hitherto referred to the genus *Bathygadus*—viz., *B. longifilis*, Goode and Bean ‖—having the scapula perforate. This species also differs from *Bathygadus* in the presence of a slit behind the fourth gill, and I propose to make it the type of a new genus *Gadomus*; it is worth noting that this is undoubtedly a very generalized Macrurid, as is shown by the terminal mouth, cycloid scales, subcontinuous dorsal fins, and the first dorsal

* Cat. iv. p. 317 (1862), and 'Study of Fishes,' p. 537 (1880).

† Vol. iii. pp. 2453, 2528, and 2602.

‡ Ann. & Mag. Nat. Hist. (7) viii. 1901, p. 261, and x. 1902, p. 295.

§ 'Southern Cross' Fishes, p. 177.

‖ *B. multifilis*, Günther, and *B. furvescens*, Alcock, are identical with this species. *B. melanobranchus*, Vaillant, has a slit behind the fourth gill and the foramen between scapula and coracoid; I propose for it the generic name *Melanobranchus*.

ray articulated, and there can be little doubt that the foramen between scapula and coracoid is a specialization which has independently arisen within the Gadoid group, and does not indicate affinity with other fishes in which this specialization has also arisen, concurrently with the forward shifting of the ventral fins.

Since, then, the position of the scapular foramen cannot be used as an absolute character for separating the Gadoids from the Zoarcidæ, Brotulidæ, &c., other distinguishing features must be found if these families are not to be associated in the same group; and after examining all the skeletons available, and in several cases making dissections, it appears to me that the following generalizations hold good :—

In the Gadoids (Gadidæ and Macruridæ) the ventral fins consist of 1–12 soft rays and are below or in front of the pectorals, whilst the pelvic bones are posterior to the clavicular symphysis, to which they are loosely attached by a ligamentous connexion; the first two vertebræ have no epipleurals, the first epipleural being attached to the first rib.

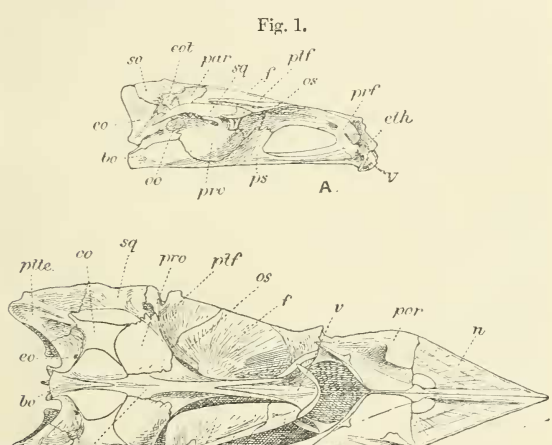
In the Blennioids (Blenniidæ, Zoarcidæ, Brotulidæ, Ophidiidæ, &c.) the ventrals, when present, consist of less than 5 soft rays, sometimes with the addition of a spinous ray, and are jugular, the pelvic bones being directly and firmly attached to the clavicular symphysis; whilst the first two vertebræ bear sessile epipleurals.

It is evident that the Blennioid fishes are modified Acanthopterygii, but that the Gadoids have originated from some less specialized stock, and that the absence of non-articulated fin-rays, the large number of rays in the ventrals, and the lack of direct attachment of the pelvic bones to the clavicles, taken together, must be regarded as primitive features. From their anatomy and appearance I am inclined to think that the Gadoids are not related to the Percesoces, but are derived from some Haplomous stock from which the Berycidæ have also descended, and of which the Stephanoberycidæ may well be the living representatives. They may be distinguished from the Percesoces by the extreme development of the opisthotic, which forms a large part of the lateral wall of the brain-case and extends down to the basioccipital, thus separating the pro-otic from the exoccipitals. In most Teleostei the exoccipital extends forward below the opisthotic and meets the pro-otic *.

* Exceptions are the Fierasferidæ and Gobiidæ, in which the opisthotic has the same relation as in the Gadoids (see Emery, 'Fauna und Flora des Golfes von Neapel,' *Fierasfer* (1880); but in other characters these three groups are widely different.

Most of the Gadoids can be referred to one of two families, viz. Macruridæ, with ventrals below the pectorals and with tapering tail, without separate caudal fin, and Gadidæ, with ventrals anterior to the pectorals and with a distinct caudal fin, which is, however, secondary, symmetrical, and composed mainly of dorsal and anal rays.

Fig. 1.



A. Skull of *Brotula multibarbata*, seen from the side.
B. Skull of *Trachyrhynchus trachyrhynchus*, seen from below.

bo., basioccipital; *eo.*, exoccipital; *so.*, supra-occipital; *eot.*, epiotic; *oo.*, opisthotic; *pro.*, pro-otic; *par.*, parietal; *f.*, frontal; *ptf.*, postfrontal; *prf.*, præfrontal; *sq.*, squamosal; *os.*, alisphenoid; *ps*, parasphenoid; *eth.*, ethmoid; *v.*, vomer; *n.*, nasal; *pal.*, palatine; *por.*, præorbital; *sor.*, suborbitals; *entp.*, entopterygoid; *ectp.*, ectopterygoid; *q.*, quadrate; *pop.*, præoperculum; *ptte.*, post-temporal.

In the Macruridæ I would provisionally include *Melanonus*, a genus known only from one specimen and placed by Dr. Günther* in the Gadidæ. It differs from most Macrurids in its only moderately elongate body, in having

* 'Challenger' Deep-sea Fishes, p. 84, pl. xiv.

vomerine and palatine teeth and a single continuous dorsal fin. *Lyconus*, regarded by Dr. Günther * as the type of a distinct family on account of the undivided dorsal and the presence of pseudobranchiæ, should also be placed in the Macruridæ.

In the Macruridæ we pass from the more generalized forms with cycloid scales, terminal mouth, and continuous or subcontinuous dorsal fins, to those with rough or spinous scales, inferior mouth and projecting snout, and a well-differentiated anterior dorsal. In these latter the snout is formed by the enlarged nasal bones, which unite in the middle line, and are supported below by the united præorbitals; in them also the suborbitals are enlarged and angulated, their upper portion forming an oblique shelf supporting the eye. This feature is most distinct in the genus *Trachyrhynchus*, which represents the extreme of specialization, and in which the posterior suborbitals extend back and join the præoperculum, and there is no trace of a median suture between the frontals. The post-temporal of *Trachyrhynchus* is also peculiar, as in addition to the two forks which are attached to the epiotic and opisthotic there is a third which runs to the exoccipital, and the interspaces between all three are filled in by an osseous membrane, so that it appears to form an integral part of the skull, and has, indeed, been mistaken by Supino † for the opisthotic.

Specialization within this family would seem to have been accompanied by an increase in number of the pectoral pterygials, for whilst *Bathygadus* and *Gadomus* have three and *Macruronus* four, in *Hymenocephalus* there are five, and in *Macrurus*, *Coryphænoides*, and *Trachyrhynchus* six. The extreme interest of the genus *Macruronus*, represented by a single species, *M. novæ-zealandiæ*, has not yet been appreciated. Although a true Macrurid in the position of the ventrals and the absence of a caudal fin, it is at least as nearly related to the Gadid genus *Merluccius* as to any member of its own family (the evidently closely allied *Steindachneria* excepted). The appearance of the head, with the wide terminal mouth, strongly toothed jaws, &c., is exactly that of a *Merluccius*;

* 'Challenger' Deep-sea Fishes, p. 158, pl. xlii.

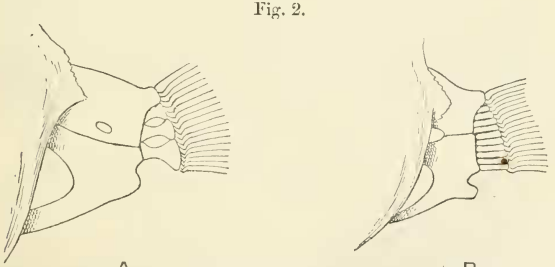
† "Ricerche sul Cranio dei Teleostei, II. *Macrurus*" (Ric. Lab. Anat. Univ. Rom. ix. fasc. 2–3, 1902). In this paper the sutures are not too accurately depicted; as has been said, the post-temporal is mistaken for the opisthotic, and the large opisthotic has not been recognized. The nasal bones are named "mesethmoid," and a pair of inferior frontal ridges "orbitosphenoid." Moreover, I cannot find any trace of a basisphenoid in this species or in any fishes of this suborder.

and this correspondence extends to minute structural details, the upper surface of the skull being precisely similar in both, and unlike that of any other Gadoid, in having a pair of divergent frontal ridges, starting from the supra-occipital crest, and enclosing a large triangular depression. *Macruronus* differs from the Macruridæ and resembles the Gadidæ in the intimate union of the first vertebra to the skull, whilst its neural spine is directly and firmly attached to the supra-occipital crest. Moreover, in both *Macruronus* and *Merluccius* the frontal bones are paired, the pectoral pterygials are four in number, the vomer is toothed, the scales are small and cycloid, concealed glandular pseudobranchiæ are present, and the dorsal fin has an elevated anterior portion composed entirely of articulated rays and subcontinuous with the rest of the fin.

The vertebral column in *Macruronus* is quite normal, the parapophyses being only moderately expanded, and bearing ribs, whereas in *Merluccius* the anterior vertebræ only bear ribs, the other præcaudals having strong and much expanded parapophyses, without ribs.

Messrs. Jordan and Evermann* make *Bregmaceros* the type of a distinct family, which they place near the Brotulidæ, on account of the supposed similarity in the structure of the pectoral arch. I find that this genus is typically Gadid, the foramen being between scapula and coracoid, the pelvic bones free from the pectoral arch, and the caudal fin symmetrical.

Fig. 2.



Diagrams showing the relations of scapula, coracoid, and pterygials in (A) *Ganonus longifilis* and (B) *Muræolepis marmoratus*.

The genus *Muræolepis*, represented by a single species,

* Fishes N. Am. iii. p. 2526.

M. marmoratus, known only from two specimens from Kerguelen, was placed by Dr. Günther* in the Gadidæ. It is a highly specialized type, whose nearest relations are with the Gadid genus *Onos*, which it resembles in general appearance, as well as in the composition of the fins, the structure of the skull, and the dentition. The foramen is between scapula and coracoid, but the pterygials are no less than ten in number. The gill-membranes are united, but free from the isthmus, and the gill-openings are restricted from above, commencing below the level of the pectorals. The scales are peculiar, being oblong and arranged at right angles to each other, much as in the Anguillidæ or in some species of *Ophidium*; there is no distinct caudal fin. All these features indicate so considerable a differentiation from the Gadidæ that this genus might well be considered as the type of a distinct family. In his generic diagnosis Dr. Günther states that the air-bladder has a pneumatic duct; the anterior part of the air-bladder is very muscular and the so-called duct is probably a vascular and nervous strand supplying this muscular portion.

The suborder Anacanthini and its component families and subfamilies may be defined as follows :—

Suborder Anacanthini†.

Parietals separated by the supra-occipital; pro-otic and exoccipital separated by the enlarged opisthotic; pectoral arch attached to the skull; no mesocoracoid; no infra-clavicle. Vertical and ventral fins without spinous rays (except the first dorsal ray of some Macrurids); ventral fins anterior in position, the pelvic bones posterior to the clavicular symphysis and only loosely attached to it by ligament. Gills pectinate. Air-bladder without pneumatic duct.

Family 1. Macruridæ.

Suborbitals not forming an internal subocular lamina. Post-temporal forked, attached to the epiotic above and the opisthotic below.

* 'Challenger' Shore-Fishes, p. 18, pl. viii.

† Certain features of the suspensory apparatus seem to be constant throughout the suborder, and may prove to be of some importance. The head of the hyomandibular articulates within a single socket, to the formation of which the squamosal and postfrontal contribute. The entopterygoid is well developed, attached to the ectopterygoid below and in front by a vertical suture to the palatine. The palatine is attached anteriorly only to the præfrontal, and has a long maxillary process.

Basis cranii simple. Vertebræ numerous, the first two without parapophyses, ribs, or epipleurals, those following without parapophyses and with sessile ribs to which epipleurals are attached, most of the præcaudals with well-developed parapophyses, bearing ribs, the epipleurals attached either to the ribs or the parapophyses. Anterior caudal vertebræ with much enlarged hæmal canal. Pectoral pterygials 3–6 in number. Foramen between scapula and coracoid (except in *Gadomus*). Gills four, a slit behind the fourth (except in *Bathygadus*); gill-openings wide, the membranes free from or narrowly joined to the isthmus; 6–8 branchiostegals; pseudobranchiæ, if present, usually glandular, reduced. Mouth protractile, terminal or inferior. Body elongate, tapering, without distinct caudal fin; dorsal and anal fins long, confluent posteriorly, the former with or without a separate anterior portion; ventrals below the pectorals, with 7–12 rays. A mental barbel usually present.

Subfamily *Bathygadinæ*.

The first vertebra articulating normally with the skull, its neural spine not directly attached to the occipital crest. First dorsal ray not spinous. First gill-arch entirely free anteriorly.

Genera:—*Melanonus*, *Lyconus*, *Gadomus*, *Bathygadus*, *Melanobranchus*, *Trachyrhynchus*.

Subfamily *Macrurinæ*.

Differ from the preceding in that the epibranchial and lower part of the ceratobranchial of the first gill-arch are connected by membrane to the wall of the gill-chamber, leaving only a narrow slit in front of the first gill. The first dorsal ray is a non-articulated spine.

Genera:—*Hymenocephalus*, *Malacocephalus*, *Macrurus*, *Coryphænoides*, &c.

Subfamily *Macruroninæ*.

Neural arch of first vertebra suturally united to exoccipitals and its neural spine directly and firmly attached to the supra-occipital crest. In other respects like the Bathygadinæ.

Genera:—*Macruronus*, *Steindachneria*.

Family 2. Gadidæ.

Closely allied to the Macruroninæ, from which they differ

only in the more anterior ventrals, which have 1–9 rays, and in having a separate caudal fin. Frontal bones united to form an undivided plate (except in *Merluccius*), as in the more specialized Macruridæ. Vertebral column as in the Macruridæ (except in *Merluccius*, in which ribs are absent from the vertebræ with the strong expanded parapophyses). Pectoral pterygials 4–5 in number. Scales small, cycloid. Dorsal and anal fins often divided into two or three portions. A mental barbel usually present.

It has already been pointed out by Mr. Boulenger * that the Gadidæ must be derived from fishes like the Macruridæ which have lost their caudal fin, as otherwise the structure of the Gadid caudal, which is symmetrical, and supported by the neural and hæmal spines of the posterior vertebræ, and by basal bones similar to those supporting the preceding dorsal and anal rays, is inexplicable. The Macruridæ, although including many very aberrant types, are, in the two essential characters of the more posterior ventrals and absent caudal, less specialized than the Gadidæ, which latter are connected with the more generalized Macrurids through *Macruronus*.

Genera:—*Merluccius*, *Gadus*, *Halargyreus*, *Lotella*, *Phycis*, *Physiculus*, *Haloporphyrus*, *Lota*, *Molva*, *Onos*, *Bregmaceros*, *Brosmius*, *Raniceps*, &c.

Family 3. Murænolepididæ.

Closely related to the Gadidæ, from which they differ in not having a separate caudal fin, in the gill-openings restricted to below the base of the pectorals, in the increased number (ten) of the pectoral pterygials †, and in the peculiar scales, similar to those of the Anguillidæ. Ventrals with 5 rays. A mental barbel. Frontals forming an undivided plate.

Genus:—*Murænolepis*.

* Ann. & Mag. Nat. Hist. (7) x. 1902, p. 295 *et seq.*

† The increased number of pectoral pterygials has been regarded by Sagemehl (Morphol. Jahrb. x. 1885, p. 17) as indicating generalization, and has been a great stumbling-block in his discussion of the affinities of *Gymnotus* with the other Ostariophysi, and especially the Characinidæ. The fact, as Mr. Boulenger has pointed out to me, that the same feature is repeated in three such distinct families as the Gymnotidæ, Anguillidæ, and Murænolepididæ, and occurs in genera which are in all other respects more specialized than their neighbours, goes far to prove that Sagemehl was mistaken in his interpretation of this character.